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History and Present State of the Odd-Year Pink Salmon Runs of the Fraser River Region

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ABSTRACT

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During 1901-13 the average number of odd-year pink salmon in the Fraser region is estimated to have been about 48 million, of which 37 million came from above the river's canyon and 11 million were from the lower Fraser and small adjacent streams. The upriver stocks were exterminated by railway construction in 1913, and did not begin to recover until a fishway was constructed in 1945. From 1915 onward the downriver runs have supported a fishery whose catches have fluctuated in response to two cycles of overfishing followed by reduced fishing. The abundance of these stocks reached a low point of 2 million in 1961, while the recent high was about 17 million in 1985, with superimposed smaller changes presumably due to variations in ocean conditions. The average individual size of Fraser pinks has decreased by 0.64 kg, or 23%, from 1951 to 1987. During this interval ocean temperatures decreased to 1975 and then increased sharply. While pinks of small populations tend to be larger than those of adjacent more numerous populations, this effect does not account for the sustained decline in size. The only known effect that has been unidirectional over the whole period in question is the selective removal of larger individuals by the gillnet and troll fisheries, which is quantitatively capable of causing an hereditary decrease in rate of growth of the observed magnitude. Since 1945 the principal pink runs to the upper Fraser have reestablished themselves naturally, but they have failed to regain their former abundance, either absolutely or relative to downriver runs. Possible reasons for a lower productivity of these stocks include the unavoidable dissipation of energy and substance during their longer migrations through violent rapids, for which they have a greater maximum swimming speed than downriver pinks; the increasing difficulty of that migration due to decreasing individual size; more severe natural conditions, upriver, for reproduction and survival of fry; and human damage to some spawning streams.

RÉSUMÉ

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Pendant la période 1901-1913, on estime à environ 48 millions l'effectif moyen des saumons roses des années impaires dans la région du Fraser. Sur ce total, 37 millions venaient de l'amont du canyon et 11 millions du cours inférieur du fleuve et des petits affluents. Les stocks d'aval ont été détruits par la construction du chemin de fer en 1913, et n'ont commencé à se rétablir qu'après la création d'une échelle à poissons en 1945. A partir de 1915, les remontes d'aval ont fait l'objet d'une pêche dont les prises ont fluctué en réaction à deux périodes de surexploitation suivies d'une réduction de la pêche. L'abondance de ces stocks a atteint un plancher de 2 millions en 1961, alors qu'on a observé en 1985 un sommet de 17 millions environ, les faibles fluctuations notées entre temps étant probablement dues à la variation des conditions océaniques. La taille moyenne individuelle des saumons roses du Fraser a diminué de 0,64 kg, soit 23%, entre 1951 et 1987. Pendant cet intervalle, les températures de l'océan ont baissé jusqu'en 1975 pour ensuite augmenter fortement. Bien que les saumons roses des petites populations soient en général plus gros que les membres des populations adjacentes plus nombreuses, cet effet ne permet pas d'expliquer la baisse régulière de la taille. Le seul effet connu qui se soit manifesté de façon unidirectionnelle pendant toute la période considérée est le prélèvement sélectif d'individus de grande taille par les pêches au filet maillant et aux lignes traînantes, que est quantitativement capable de causer une réduction héréditaire du taux de croissance d'une ampleur correspondant à celle du phénomène observé. Depuis 1945, les remontes principales de saumons roses du cours supérieur se sont rétablies de façon naturelle, mais elles n'ont pas retrouvé leur abondance d'autrefois, ni dans l'absolu ni par rapport aux remontes d'aval. On peut expliquer la plus faible productivité de ces stocks par la dissipation inévitable d'énergie et de substance pendant leurs longues migrations dans des rapides violents, où ils doivent user d'une vitesse maximum de nage supérieure à celle des saumons roses de l'aval; par la plus grande difficulté de cette migration due à la réduction de la taille des individus; par la plus grande dureté des conditions naturelles, en amont, en ce qui concerne la reproduction et la survie des alevins; enfin, par la dégradation de certaines frayères du fait de l'homme.

1. CHANGES IN ABUNDANCE

1.1. EXTERMINATION OF THE UPRIVER PINKS IN 1913

Pink salmon (*Oncorhynchus gorbuscha*) of the Pacific Ocean have a 2-year life history almost without exception. In even-numbered years pinks are very scarce in the Fraser River and most adjacent streams of the lower Strait of Georgia and Puget Sound, but are abundant in odd-numbered years -- a situation which has existed from the time of the region's first historical records during the 19th century. Several possible reasons for this remarkable alternation (which occurs also in some other pink salmon regions) have been outlined by Ricker (1962) and others. However, the present paper is concerned only with the odd-year stocks.

The early history of the pink salmon runs and fisheries of Puget Sound and the Fraser River was brought together in the great monograph by Rounsefell and Kelez (1938), in which the sections concerning pink and sockeye salmon were written by the late Dr. George A. Rounsefell. The original numbers of both of these species in their cyclic "big" years was so great that it is difficult to relate them to modern concepts. Much of the largest pink salmon stocks ran to sites above the Fraser canyon. There the main spawning stream was the Thompson River, including its main stem, its South Branch, and probably also its North Branch. In addition the Seton-Anderson system and the Nicola River were both said to contain "millions" of pinks. Smaller numbers entered tributaries of the Fraser at least as far upstream as Quesnel River, and tributaries of the Thompson up to the south end of Shuswap Lake, where the hatchery sometimes took eggs from pinks in Granite Creek near Tappen, not far from Salmon Arm. Pinks may also have spawned in the less rapid portions of the upper Fraser itself, as they do in the main stream below the canyon, but if so they escaped notice in its muddy water.

However, the abundance of pinks decreased abruptly after 1913, when obstructions in the Fraser River canyon, especially at Hell's Gate, prevented access to all these upriver spawning areas. In 1913 no pinks at all were reported above Hell's Gate by Babcock (1914) or Mitchell (1925), and the runs were not restored in subsequent years.

1.2. ABSOLUTE ABUNDANCE OF ODD-YEAR PINKS DURING 1901-13

Rounsefell and Kelez (1938, Table 52) computed an index of pink salmon abundance from the catches of traps at long-established sites north of Deception Pass, which separates Fidalgo and Whidbey Islands. These caught pinks that were bound mainly for the Fraser and a few much smaller nearby streams, especially the Nooksack in Washington and Indian River in British Columbia. The indices for odd-numbered years are shown in Table 1.

I see no reason to doubt that these indices are a reasonably good reflection of the abundance of pink salmon over the period in question. Trap construction changed little from the turn of the century onward. Any minor alterations, as time went on, would naturally be improvements, which would tend to make the change in the index of abundance, from early to later years, *less* than the actual decrease in numbers.

The ratio of the means of the northern trap indices during the four generations immediately before and immediately after the effects of the 1913 obstructions is 281.5:64.5, so that mean abundance was reduced to only 23% of what it was previously. This in turn suggests that the region above Hell's Gate contributed 77/23=3.3 times as much to the catch of these traps as did the Fraser below the Gate and neighbouring streams.

It is impossible to translate these figures directly into actual numbers of fish, because complete catch statistics are not available for earlier years and rates of utilization then are not known. However, the average odd-year catch for the whole Fraser and Puget Sound region is given by Rounsefell and Kelez (1938, Table 47) as 10.94 million fish in 1925-31, and the mean northern trap index was 73.8 for those years. For an estimate of the rate of utilization, note that the years 1971-83 resemble 1925-31 in that pink populations of the region were at about the same level, with an upward trend in both cases (Tables 2 and 3, Fig. 1). In 1971-83 the mean rate of utilization of Fraser pinks was 74.1% (column 15 of Table 3), so we can conclude that for 1925-31 it was probably about the same. It would certainly not have been as large as the 83% of 1959, which was followed by the collapse of the stock. However, the 74.1% figure is for Fraser pinks only, and the Puget Sound pinks had a consistently lower rate of utilization, presumably because of the absence of important river fisheries. Thus, the best estimate of the overall rate of utilization in 1925-31 is likely to have been about 70%. For our purpose the exact value is not critical; in

fact any figure between 0 and 100% will indicate a very large upriver pink population in the computation below.

Taking the average rate of utilization in 1925-31 as 70%, the average total pink run then was 10.94/0.70 = 15.6 million. Allowing 20% of these for streams south of Deception Pass, this means that about 12.5 million pinks were being produced per odd-numbered year in the Fraser and adjacent streams. Average abundance in these waters in 1915-21 would then be, from Table 1, 12.5 X 64.5/73.8 = 10.9 million. Finally, the mean abundance in 1907-13 in the same waters can be estimated as 10.9 X 281.5/64.5 = 47.7 million. Of these 47.7 X (281.5 - 64.5)/281.5 = 37 million were from above Hell's Gate, and the remaining 11 million from the lower Fraser and adjacent streams.

1.3. REESTABLISHMENT OF UPRIVER RUNS AFTER CONSTRUCTION OF FISHWAYS

The upriver spawning areas became accessible to pinks again in 1945, when the International Pacific Salmon Fisheries Commission completed its first fishway at Hell's Gate. In 1947 about 2,000 pinks were observed spawning in Seton Creek, probably mainly the progeny of strays from downriver runs that had reached there in 1945. By 1949 pinks were reported in the Thompson and Nicola Rivers as well. Since then they have increased moderately (column 6 of Table 3). The largest recent estimate was 1.79 million in 1981, but this was followed by a disappointing 1.10 million in 1983 and only 0.47 million in 1985; however it rose again to 1.05 million on 1987.

2. REACTION OF PINK SALMON TO OBSTRUCTIONS

2.1. SUSTAINED EFFECTS OF 1913-14 OBSTRUCTIONS AT HELL'S GATE

J. P. Babcock (1914) surveyed the Seton Creek spawning grounds in 1913, and found no pink salmon at all, where formerly there had been hundreds of thousands at least, probably millions. Similarly Mitchell (1925) reported that the enormous runs to the Thompson River and tributaries disappeared in 1913. Moreover, the remedial works at Hell's Gate and elsewhere in the canyon,

done in 1914-15, did not permit any appreciable number of pinks to get upriver, even though they permitted all but a small fraction of the sockeye to get through after 1914 (Ricker 1987). A few pinks did get past the Gate in some years. Babcock (1924) reported them in 1923 at Seton Lake and in the Thompson River, and Fishery Guardian W. P. Forsythe of Alexis Creek told me that in 1937 he saw a few pinks at Farwell Canyon in the Chilcotin River. Female sockeye salmon were much less successful than males in passing natural obstacles, both on the Fraser and at Babine River (Ricker 1987). Presumably the same would be true of pinks, and Williams et al. (1986) showed experimentally that female pinks have a lower maximum swimming speed than do the males, partly because of their smaller average size (see Section 4). Thus it must have been mainly or exclusively male pinks that occasionally got through Hell's Gate during 1915-43; at any rate no upriver spawning was reported anywhere during those years.

2.2. COMPARISON WITH BABINE RIVER PINKS

It is of some interest to compare the Fraser pinks with those of the upper Babine River, which were also affected by obstructions, in 1951 and 1952. Of course the pink run that reached the fence below Babine Lake was never large in absolute terms. Godfrey et al. (1954) give the fence counts as follows:

Before the slide		Slide years	
1946	28,161	1951	50
1948	55,421	1952	2,706
1949	13,663		
1950	38,728		
Mean	33,993	Mean	1,378

This suggests that about 4% of the pinks passed the slide. Godfrey et al. also gives the fence counts in terms of a percentage of the catch in each year, and on this basis the 1951-52 arrivals averaged less than 1% of the mean of the previous 4 years. Whichever index is used, it is clear that pinks were much less successful than sockeye in passing the Babine slide, because about 33% of the sockeye escapement ascended the slide and reached the fence both in 1951 and 1952 (Godfrey et al. 1954).

Thus, both the Fraser and the Skeena pinks were much less capable of coping with an obstruction than were the sockeye.

But whereas the abundance of the Babine pink run was restored in a few generations after the slide was removed, the Fraser pink salmon continued to find Hell's Gate almost impassible right up to the time fishways were built in the 1940s.

3. THE COMMERCIAL FISHERIES

3.1. HARVESTING AND OVER-HARVESTING

The history of the Fraser and Puget Sound pink salmon fisheries suggests that overfishing did not occur until the 1930s (Tables 2 and 3). Although Rounsefell and Kelez (1938) were able to assemble reasonably complete catch statistics for pinks only from 1925, their comments and the incomplete figures in their Tables 48 and 49 indicate that packs were small before the war of 1914-18, mainly because pinks were not highly esteemed. Largest quantities were taken in the odd-numbered "off" years of the sockeye salmon cycle, that is, in 1903, 1907, etc. This was because pinks were very scarce in even-numbered years, while in the "big" sockeye years (1901, 1905, etc.) there were more than enough of that much more valuable species to saturate canning capacity throughout most of the fishing season. Thus, the very large supplies of pinks available in odd years through 1913 were only lightly used.

During the war of 1914-18 demand for pinks increased, and the supply was of course much less than previously. However, a decline in the pack in 1919 and 1921 probably reflected the business recession rather than decrease in the number of fish. By the middle 1920s business had improved and new markets for pinks were found. The catch by Canada and the United States averaged 10.9 million pieces in the odd years 1925-31 (Table 2). The trap index in Table 1, for the region north of Deception Pass, showed little sign of any downward trend after 1915 until the last year, 1933, when its lowest value was recorded. After 1933 the trap index is no longer available, but its low value in 1933 is matched by a 35% decrease in the total catch of the region, to 8.2 million. This was followed by three additional years of declining catches, reaching 5.3 million by 1939 (Table 2). Part of this continued decrease was a result of the removal of traps from Washington waters after 1933. However, Table 2 shows that the Canadian pink catch increased very little as a result -- unlike the Canadian sockeye catch, which

immediately increased more than 3-fold while the United States catch decreased to less than half. Thus, an important decrease in the total run of pinks evidently occurred during the 1930s, starting with the low index for 1933.

If the pink salmon fishery had been the responsibility of a single regulatory body at that time, very likely more spawners would have been permitted to escape. However, there was as yet no mechanism for international control of fishing. The International Pacific Salmon Fisheries Commission was established late in 1937, but it was to deal with sockeye only, and even for that species it was not empowered to set regulations until 1946. It is of course possible, though unlikely, that an environmental fluctuation was mainly responsible for the reduced abundance of pinks during the 1930s. However, there was no indication of unusual oceanographic conditions; and the Fraser sockeye catch did not decrease, indeed most of its upriver stocks were increasing rapidly (Ricker 1987). In any event, a temporary decline in natural survival rate makes it all the more necessary to decrease the percentage of a stock that is harvested, so as to have adequate spawning.

3.2. REDUCTION OF FISHING DURING THE 1940s

Fortunately for the pinks, war broke out in 1939, and two years later there had been a marked decrease in fishing effort, mainly attributable to restrictions on and the eventual relocation of fishermen of Japanese descent. Catches decreased to 3.6 million in 1941 and 1.3 million in 1943. Thus, the pink stocks gained an important respite. With increased fishing after the war, the catch rose to an average figure of 9.9 million during 1947-51.

3.3. POST-WAR EXPANSION OF FISHING AND DECREASE IN ABUNDANCE TO 1961

From 1915 through the 1940s United States fishermen had been taking more than two-thirds of the region's pink catch (Table 2), and they were unlikely to consent to a catch-sharing agreement on a 50:50 basis as long as this continued. So during the early 1950s Canada's industry was encouraged to increase its seine fishery in the Strait of Juan de Fuca. This tactic was successful, in that the catches of the two countries were almost

equal by 1955 (Table 3), and the United States then agreed to put recommendations for management of all the pink fisheries in this region into the hands of the International Pacific Salmon Fisheries Commission, starting in 1957. This common plan included a 50:50 division of the catch as nearly as was practical -- something the Commission was already doing for sockeye salmon.

Unfortunately, Canada's extra effort had not increased the combined catch of the two countries. Instead, the catch fell from 12.3 million in 1947 to 9.1 million in 1953 and 8.8 million in 1955 *in spite of the increased fishing effort*; which meant that spawning stocks were being reduced at a rate greater than the decrease in the catch. This was a signal of almost certain overfishing, so that when the Commission assumed responsibility for management in 1957, some relaxation of fishing intensity was clearly indicated. Instead, of the 9 million or so pinks that appeared in 1957, only 2.25 million spawned in the Fraser system, and spawners in other rivers would add no more than 0.5-1 million. Again in 1959, instead of moderating the fishery, the rate of utilization was allowed to increase still further: there were about 7 million fish in all, but only 1.1 million Fraser spawners. Then came the disastrous year 1961, when not more than 2.2 million pinks appeared. However, the Commission had finally become sufficiently alarmed to recommend severe restrictions on fishing during the pink run, and about half of these fish were allowed to spawn.

3.4. LARGER ESCAPEMENTS AND INCREASED ABUNDANCE OF RECENT YEARS

The pinks spawned in 1961 had an unusually good survival rate, especially those in Puget Sound streams, but this was followed by poor survival in the next generation. In 1967 a good run returned, but an 86% exploitation rate again pushed the Fraser spawning stock down to a rather low level (1.83 million).

In the years since 1967 the Commission has successfully restrained the fishery in its Convention area, but two new developments have complicated the situation. Starting in the late 1950s, trollers learned how to catch pink salmon in numbers, and those operating off Washington and Vancouver Island increased their share of the total catch of Fraser-Puget pinks to 30-40% in 1977-81 (IPSFC Annual Report for 1981, Table 7). In 1983 their catch was apparently 2.5 times as large as the inside catch -- whose fishermen had to bear the brunt of the conservation regulations. Another development has been that in some recent years, notably 1983, a substantial number of Fraser pinks have

migrated south through Johnstone Strait, where many were caught along with fish from local Strait stocks. But one way or another the rate of utilization of Fraser pinks was held close to 70% during 1973-85 (Table 3), and Fraser spawning stocks gradually increased. The recent maximum spawning was 6.5 million in 1985, but after poor survival of that brood only 7.1 million in all arrived in 1987, of which 3.2 million got to the spawning grounds. Such fluctuations are to be expected. What is disappointing is that the stocks above the canyon have not increased nearly as much as had been hoped for on the basis of their former abundance.

4. SIZE OF FRASER-PUGET PINK SALMON

4.1. DECREASE IN SIZE SINCE 1950

A disturbing feature of the region's pink populations since 1950 has been a decrease in the average size of the individual fish. The Juan de Fuca (Area 20) seine catches are probably most representative of size for the region as a whole. Their mean weights for 1951-75 were shown by Ricker, Bilton and Aro (1978) in their Table 4 (column 3 of Table 4 here), and they computed the average linear decrease to 1975 as 0.27 kg, or 11% of the initial weight in 12 generations. Very similar weights appear in the Salmon Commission's Fraser size index, which starts in 1959; it is based on seine catches near Point Roberts (column 6 of Table 4). Both series indicate new record lows for 1979 and 1983, followed by an increase in 1985 and decline in 1987. Using the Point Roberts index along with the years 1951-57 from Juan de Fuca, the computed linear decrease is now from 2.83 to 2.19 kg in 18 generations, a decline of 0.64 kg or 23%, or 36 g per generation (Fig. 2).

4.2. EFFECTS OF THE OCEAN'S CLIMATE

In searching for causes of this decline, a natural first suspect must be changes in oceanic conditions. Ricker et al. (1978) noted that the size decrease during 1951-75 coincided with a sustained cooling trend in the northeastern Pacific Ocean, and a test for causation was made by comparing the yearly anomalies of size and of temperature computed from their

respective linear trends. In southern British Columbia (Districts 1 and 3) there were no "significant" relationships between these anomalies, although most were positive. But even assuming this to be meaningful, the rates of decrease in size computed from the observed regressions were much less than the observed rates (Ricker et al., Table 22). Since 1975, of course, ocean temperatures have increased abruptly to record high levels, while the size of the Fraser pinks has continued to decrease, so a monotonic relation between size and temperature can be ruled out.

This is not to say that ocean conditions do not affect pink sizes. Most of the year to year fluctuations about the trend line must have this cause, and occasional severe effects are to be expected. The 1983 Report of IPSFC suggested that year's record small size (2.03 kg) might have been associated directly or indirectly with the "El Niño" warming. However, El Niño has since shifted back to the cooler "La Niña" situation, but pink sizes have increased only slightly (Fig. 2). In northern British Columbia and southeastern Alaska the decline in size of odd-year pinks was interrupted by an increase in 1977-81 (Ricker 1984; Healey 1986), which may well have been a result of the rise in temperatures; but their decline was resumed in 1983-85 (Marshall and Quinn 1988; CDFO Statistics). In any event there was no similar temporary improvement in southern British Columbia.

4.3. RELATION BETWEEN SIZE AND ABUNDANCE

Another possibility is that pink sizes could be related to their numbers. Figure 6 of the IPSFC Report for 1983 relates size to the abundance of Fraser pinks from 1959 to 1983. The relation is negative and somewhat curved. In Figure 3 here the points for 1985 and 1987 are added, of which the latter lies below the previous range of scatter at that level of abundance.

An inverse relation between size and abundance of pinks is reasonable, and small size has been observed to accompany unusual abundance in at least two other statistical Areas of British Columbia -- Area 8 in 1968 and Area 6 in 1972 (Ricker 1984). The relationship probably results mainly from competition for food during the coastal period of the life of the fish, before they move out to the high seas. However, there was also a general decrease in size of odd-year pinks in the central and northern Areas (District 2) of the British Columbia coast during 1951-75, where their abundance, as indicated by catches, did not

increase but instead *decreased* by more than 50% (Ricker et al. 1978, Tables 3, 4 and 9). (Pinks of the District 2 even-year stocks decreased even more in size, while their catches remained about the same.) Note also that the runs of 1951-55, when Fraser-Puget pinks numbered about 11-13 million, consisted of much larger individuals (Area 20 seine average, 2.83 kg) than did runs of similar abundance in recent years (average for 1967, 1971, 1977 and 1979, 2.38 kg). It would be most interesting to know the mean size of the pinks in the very large Fraser populations that existed before 1915.

4.4. DIRECT EFFECT OF FISHING

Another contribution to the decrease in size of the Area 20 seined pinks may have been made by the outer troll fishery, which captures larger pinks than seines do in most areas where both gears operate (Table 4 of Ricker et al. 1978). However, the same Table shows that the pinks caught by troll off Vancouver Island (Areas 21-27) differed little in average size from the seine-caught pinks of Juan de Fuca (Area 20). In any event the mean size of odd-year pinks caught by all gears combined, in southern British Columbia, continued to decrease through 1977-85 (Fig. 5 of Ricker 1984, column 7 of Table 4 here).

4.5. HEREDITARY CHANGE DUE TO SELECTIVE FISHING

Finally, a reason for decrease in size that was suggested by Ricker et al. in 1978 is that the cumulative effect of the selective harvesting of the larger pinks has been to change the population's genetic structure. That is, genes favouring rapid growth, being at a selective disadvantage, are being gradually removed or displaced by those that favour slower growth. Both trolls and gillnets usually take larger pinks than do the (presumably) unselective seines (Table 4 of Ricker et al. 1978). Although the gillnetted pinks of Area 20 are atypically small, the much greater Fraser River gillnet fishery nearly always took larger pinks than those seined in Area 20 or near Point Roberts (Table 4). And Ricker et al. (1978) showed that the required degree of heritability of factors affecting growth rate is similar to what has been observed experimentally in other fishes. This ominous scenario gains additional support from the

small size of the pinks in the rather small population of 1987 (Fig. 3).

Another result of selective fishing is that a larger percentage of the males is harvested than of the females, so that the latter can be up to twice as numerous on the spawning grounds (Fig. 4).

How much each of the various causal factors above has been contributing to the decrease in size of pink salmon in the Fraser-Puget region should become clearer as future years' data become available. But the fact of the decrease is not in question, and selective fishing is the only cause so-far suggested that has been unidirectional throughout the entire period 1951-1987.

5. PRODUCTIVITY OF UPPER FRASER PINK STOCKS

5.1. PRESENT LOW ABUNDANCE OF UPRIVER POPULATIONS

The waters above the Fraser River canyon, whose pinks were originally predominant in the region, are not yet making a major contribution to the fishery. If the reason or reasons for this can be pinned down, it may be of considerable assistance with management policies. Several possibilities can be considered.

The upriver runs would suffer greater adult mortality if they were unusually vulnerable to a particular kind of fishing, of were more prone to assemble in places where fishermen are concentrated. However, this seems unlikely because they run at the same time as the large population that spawns in the Fraser below Hope.

5.2. HUMAN DAMAGE TO SPAWNING AREAS

Some of the upriver spawning regions have worsened since the first decade of the century. The Seton Creek run is unlikely to achieve its former productive potential because most of the creek's flow has been diverted for power production. Two spawning channels have been constructed to alleviate this development, but their combined fry-producing capacity, plus that of the remaining creek spawning beds, are less than what was available in the natural state of the system. At Bridge River the diversion for power generation has made it impossible for any pink run to become established. Rock from railway construction along the Thompson and Nicola Rivers may have reduced their spawning capacity to some extent, but most of the redds are not situated where major blasting was required. Diversion of water for irrigation on such tributaries as the Nicola and the Bonaparte may have reduced their potential as spawning streams. Although it is impossible to quantify most of these changes, most of the major spawning reaches, both in the big rivers and the tributaries, are still in much the same condition as they were 80 years ago.

5.3. SMALLER NATURAL PRODUCTIVITY UPRIVER

Even without any deterioration of habitat, we probably should not expect the pink salmon above the Fraser canyon to achieve as great a numerical superiority over downriver pinks as they had before 1915. Primitive abundance must be used with caution as a guide to what fish populations can produce for a man on a sustainable basis. Although the upriver pink stocks were originally more than 3 times as large as the downriver ones, this does not necessarily mean that they will prove to be proportionally productive. In this context, productivity is defined as the ratio of a stock's maximum sustainable yield (averaged over a period of years) to its average unfished abundance. It bears no necessary relation to absolute abundance.

Typically, when a fishery reduces the size of a spawning population it increases the average survival rate of the progeny of the remainder sufficiently to produce a sustainable harvest. (No sustained harvest is possible if the original abundance of spawners is maintained, for then reproduction is so inefficient that the whole stock must take part in order to just maintain its numbers.) How large the sustainable harvest will be depends on the shape of the stock's recruitment curve.

Curve 1 of Figure 5 is a possible average recruitment curve for the present-day stocks of pinks of the lower Fraser and Puget Sound. It is constructed so that the rate of utilization (C_1D_1/B_1D_1) at maximum sustainable yield is 70%. This is approximately the mean rate of harvest of recent years. The catch is 86% of the indicated unfished level of abundance (OA). (When recruitment is affected also by year to year environmental variability, the MSY point is shifted to a position somewhat closer to the origin; see Ricker 1962.) However, we should expect the original salmon stocks in any region to include all grades of productivity, ranging from very productive ones down to those that are at the margin of the species' usable habitat. The latter will produce little or no sustainable surplus. Thus, although such stocks may initially provide large catches, these will decrease rapidly and may disappear altogether if they continue to be harvested at the same rate as more productive stocks. Curve 2 of Figure 3 is of this type. Its stock, when first fished, will provide as large a catch as Curve 1, but this quickly decreases to a maximum sustainable yield (C_2D_2) that is only 20% of the original replacement abundance (OA). To obtain this maximum sustainable yield the rate of utilization must be as small as 30%; that is, the spawning stock (OB_2) must be 2.3 times as large as the catch (C_2D_2). If the rate of utilization becomes greater than this, equilibrium yields become smaller and smaller, and a harvest of only 49% will eventually exterminate this stock. Even flatter and less productive recruitment curves are possible, of course.

In the lower Fraser and Puget Sound region the unproductive stocks have presumably been eliminated, or exist at levels very much less than their primitive abundance. The upriver Fraser runs were estimated to have originally been more than 3 times as abundant as the downriver ones (Section 1.2). But this was at a time when they were still only very lightly fished, so that their unproductive stocks must still have existed at quite high levels of abundance. Thus, we should not necessarily expect the upriver stocks to contribute to today's fishery in proportion to their earlier numbers, and their poor performance in recent years suggests that they probably will not.

5.4. ENERGY EXPENDED IN UPRIVER MIGRATION

If the pink salmon stocks above the canyon of the Fraser are really much less productive than downriver stocks, on the average, why should this be so? One possibility is fairly obvious. The upriver pinks have to expend more energy in getting to their spawning grounds. Idler and Clemens (1959) found that in travelling the 130 km from Hell's Gate to Lillooet, female *sockeye* salmon used 2.73 kilocalories per kilogram of body weight per kilometre of journey; this was mainly fat, but included some protein. The distance from the middle of the pinks' downriver spawning region in the Fraser up to Hell's Gate is about another 100 kilometres, and in this interval the river has approximately the same average velocity as from Hell's Gate to Lillooet. Pinks would have to expend somewhat more energy per kilogram than sockeye because of their smaller average size and hence less favourable ratio of surface to volume (Section 5.8); and they have in fact a higher active metabolic rate (830 mg 0_2/kg/h as compared with 750 for sockeye -- Williams et al. 1986). But using 2.73 kcal/kg/km as a minimum figure, a female Seton pink salmon weighing 2 kg would have to expend in migration more than 2.73 X 230 X 2 = 1260 kcal more energy than her downriver counterpart. This represents 136 g of fat or 307 g of protein, using Idler and Clemens' conversion factors. There are many possible alternative uses for this material. If it were all converted to eggs weighing 0.2 g each and of 75% fat content, it would mean about 780 additional eggs per female. Alternatively, it could be used to produce larger eggs, or eggs of better quality, or for more effective nest excavation, or a longer period of guarding the nest, and so on.

Spawners that go to the Thompson River beds between Spence's Bridge and Kamloops Lake have an average journey of about the same length as those that go to Seton Creek at Lillooet (see Fig. 1 of Ward 1959), but those that swim as far as the south end of Shuswap Lake, or to Quesnel on the upper Fraser, must expend considerably more energy. In summary, we should not expect upriver pinks to be as productive as the downriver stocks, simply because they have to use a lot of energy for their longer and more difficult migrations, so can invest less in reproduction.

5.5. GREATER LOSSES TO PREDATION

About other possible handicaps of the upriver pink salmon we can at present only guess. Pink fry from above the Fraser canyon of course have a much longer journey down to the sea than do those below. They are exposed to predators in the clear Thompson River, in Shuswap and Kamloops Lakes, and in Fraser tributaries like Seton, Chilcotin and Quesnel, but once into the silty Fraser predation is likely inconsequential.

5.6. ICE DAMAGE TO REDDS

Another possibility is that the upriver areas used for spawning may be, on the whole, less favourable than those available downriver. For example, the gravels may be firmer or more coarsely grained, making it difficult to excavate nests. And because larger fish are better able to dig nests into difficult bottoms, the current decrease in size of female pinks could become critical. We might also expect damage to redds from ice to be a greater hazard in the much colder winter climate above the Fraser canyon.

5.7. A HAZARDOUS DOWNSTREAM JOURNEY

There is also a possible natural source of mortality in the river itself. Those who have observed the violence of the rapids in the canyons of the Thompson and Fraser Rivers sometimes wonder how *any* pink fry, only about 3.4 cm long, could survive a journey down through them. How much, if any, damage of this sort the young fish may experience could be investigated under experimental conditions. For one thing, many of them are subject to rapid changes in pressure as the river's turbulence carries them quickly to great depths -- potentially as much as 50 meters at Hell's Gate -- or just as quickly back to the surface. Violent contact with the canyon walls and midstream rocks may also be a factor. It is known that chinook salmon smolts experience some loss in passing through even large low-speed turbines. At least part of this is from being sheared between a turbine blade and its wall, but some may result from sudden pressure change, or simply from violent turbulence.

5.8. INCREASING DIFFICULTY OF UPSTREAM MIGRATION

Finally, the canyon of the Fraser may have again become a substantial obstacle to the migration of *adult* pink salmon, as suggested on page 22 of the 1985 Annual Report of IPSFC. Although Hell's Gate is no longer a problem, there are still several rapids of formidable appearance in the canyon which may offer difficulty at certain water levels -- for example, Scuzzy Rapids and the Black Canyon. (In recent years improvement work has already been done at Saddle Rock in the Little Canyon, and is now in progress at "Little Hell's Gate".) If there is increasing difficulty of this sort, the reason may be that *pinks have become less capable of swimming up through fast water*. In Section 4.1 it was shown that between 1951 and 1987 the size of the region's pinks has decreased by 0.64 kg. D'Arcy Thompson and others have pointed out that for fish of a given shape, muscle volume increases as the cube of length, whereas surface area and hence total friction against the water increases only as the square of length. Hence, maximum swimming speed should increase approximately in proportion to length -- a rule that has been demonstrated to hold for young salmon and many other fishes (Brett 1964). Thus, a decrease in weight from 2.83 to 2.19 kg would decrease maximum swimming speed to $(2.19/2.83)^{1/3} = 0.92$, or by 8% -- a potentially critical loss in situations where the greatest possible speed may be needed. And of course many individual fish are much smaller than the average figure, and the average itself can fall well below the trend, as in 1983.

Furthermore, it is the females that are most affected by difficulties in migration, only partly because they are of a smaller average size than the males. Experiments on swimming speed were made on adult pinks of the 1983 run, and are included in the comprehensive studies by Williams et al. (1986). In their Table 15 these authors report "critical swimming speeds" achieved in 60-minute trials in tunnels, adjusted for a "blocking effect". The unit used is lengths per second (L/s), but these can be converted to actual speeds using the average sizes in their Table 14, as shown in Table 5 here. Among fish that were not yet spawning, males were better performers than females in terms of lengths per second (9% better downriver and 22% upriver), and their larger size increased their superiority in actual speed to 15% downriver and 27% upriver.

5.9. SUPERIOR SWIMMING PERFORMANCE OF UPRIVER PINKS

Less predictable, although not surprising, is the difference in performance between upriver and downriver pre-spawning pink salmon that was discovered by Williams et al. (1986). Comparing individuals of practically the same size, this amounted to 30 cm/s for females and 50 cm/s for males (Table 5). That is, the upriver females could swim 30% faster than those downriver, and the males 43% faster, even after they had already made the arduous journey up through the canyons. This difference might be a result of selection within the total early run -- upriver plus downriver -- during the 1983 season. It has in fact been suggested that the disappointing number of upriver spawners in 1983 could have been partly a result of the failure of an unusually large percentage of the upriver-bound migrants to make their way up through the fast water. However, in that event we should expect to see an unusually large percentage of males among those that did get through, whereas in fact that percentage was only about average, indeed less than the average for recent years (Fig. 4).

Another possibility is that the upriver run is genetically superior in respect to swimming speed. Because the upriver stocks were reestablished from those downriver after 1945, it is plausible, indeed almost certain, that the pioneers had a swimming capability that was better than the average in the downriver population. Since then survival of the fittest has been at work among pinks hatched upriver, and the combined result should be a series of new stocks having superior swimming performance. This process is not necessarily complete. It is being slowed by the selective removal of the larger fish by the troll and gillnet fisheries. On the other hand, small size resulting from environmental conditions in the ocean should accelerate the genetic shift by intensifying the selective process in the canyon.

A suggestive aspect of Figure 4 is that, of the three early runs, the lower Fraser has a smaller average proportion of males (37.9%) than the two upriver populations (40.4 and 41.6%), and this difference has become greater during the last 6 generations as the size of Fraser pinks has continued to decrease. This may mean that every year some of the females of the upriver populations fall back after trying to ascend the canyon, thus reducing the percentage of females upriver and, possibly, increasing their representation slightly on the spawning grounds below Hope.

It is interesting that the late-running stocks of pinks downriver have had more males than the early-run main Fraser fish: 44.4% in the Harrison River and 42.4% in the Chilliwack-Vedder. Apparently this is because they are less intensively utilized than the early run, at least by the Fraser gillnet fishery (Ward 1959, Table 4), so there is less selective removal of the males.

6. SUMMARY

Before 1915 the odd-year pink salmon of the Fraser region are estimated to have numbered about 48 million, of which 37 million were from streams above the Fraser canyon, and 11 million from the lower Fraser, its tributaries, and a few adjacent streams. Several million more spawned in Puget Sound streams from the Skagit River south. The upriver Fraser stocks were exterminated when rock dumped into the river in 1913 prevented them from getting through the canyon.

The downriver Fraser stocks maintained their numbers and provided good catches through 1931, but were reduced in abundance later in that decade, almost certainly by overfishing. They regained their numbers during the war years because of reduced fishing effort but declined again during the 1950s because of renewed attempts by both Canada and the United States to obtain a larger share of the catch. Overfishing continued for several generations even after international management began in 1957, and the stock reached an all-time low of 2.2 million in 1961. Since then strict controls have permitted a gradual decrease. The total Fraser stock was close to 19 million in 1981 and 1985, with smaller numbers in 1983 and 1987, these fluctuations being a normal result of environmental variability.

From 1951 to 1987 the average size of Fraser pinks has decreased by 0.64 kg or 23%. Ocean temperatures cannot be directly responsible, because they were decreasing from 1950 to 1975 but have increased abruptly since then, whereas the decline in size has continued. Pinks of small populations tend to be of a larger average size than those of adjacent large populations, so part of the decline in size since 1961 may be a consequence of increasing abundance. However, the large pink populations of the early 1950s consisted of large fish, and pinks of the rather small population of 1987 were small in size. The only known effect that has acted continuously in the same direction since

1951 is the selective removal of the larger fish by the gillnet and troll fisheries, and this is quantitatively sufficient to cause a steady decrease in hereditary capacity for growth of the magnitude observed.

The decrease in size of our pink salmon may be imposing increasing stress on the stocks above the Fraser canyon. These reappeared in numbers after fishways were constructed at Hell's Gate in 1945-47, but they have not yet exceeded 2 million spawners, and in 1987 numbered only 1 million. This is much less than what their pre-1915 abundance might have suggested. There have been some reduction of spawning areas upriver and possible worsening of others from man's activities, but these developments do not seem serious enough to account for the present minority position of the upriver stocks. And quite apart from any such changes, it is likely that the usable surplus or maximum sustainable yield, produced by a given number of upriver spawners, is considerably less than what is produced downriver.

For one thing, the upriver fish must expend much more energy in migration, so have less to invest in reproduction. Based on studies with sockeye, the energy expended by a 2-kilogram female salmon in swimming 230 extra kilometres up the Fraser (roughly from Agassiz to Lillooet) is equivalent to about 800 mature eggs weighing 200 mg each. Moreover, the energy expended in migration has become relatively greater as the pinks have become smaller and hence have a less favourable ratio of surface to volume. Evidence of this diversion of energy is available from 1983 experiments showing that upriver pinks were better swimmers than downriver pinks of the same size: females were 30% faster, and males 43%. This is evidently a result of selection for good performance both among the pioneers that founded the upriver stocks after 1945, and among their descendents.

Another possible reason for a smaller surplus production by upriver stocks is that their spawning beds are more subject to damage by ice; their gravel base might also be, on the average, less suitable than what is available downriver. Also, fry from upriver are more exposed to freshwater predation, and some may be killed by the violence of the rapids on their downstream journey.

All these considerations suggest that the rate of utilization that will produce maximum sustainable yield from upriver stocks may be considerably less than what is appropriate downriver, and this may well account for their failure to build up substantial populations under current fishing regimes. Unfortunately, the upriver stocks run at about the same time as

those in the main Fraser downriver, so that they are taken together in common fisheries.

7. ACKNOWLEDGMENTS

Many of the investigators who made the studies used in this paper are cited in the References. In addition, much of the information for recent years has appeared anonymously in the Annual Reports of the International Pacific Salmon Fisheries Commission, and of the Fraser River Panel of the Pacific Salmon Commission. I have also used material from a comprehensive manuscript prepared from records of the above Commissions and of the Canadian Department of Fisheries and Oceans by Dr. D. J. Blackbourn. It is only by combining the data and analyses of a great number of workers -- including many who are no longer living -- than an historical review of this sort becomes possible.

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Table 1. Rounsefell and Kelez's index of abundance of pink salmon in northern Puget Sound and southern Strait of Georgia, based on catches of traps north of Deception Pass.

1907	204		
1909	354		
1911	285		
1913	285	1907-13 mean	281.5
1915	50		
1917	89		
1919	63		
1921	56	1915-21 mean	64.5
1923	87		
1925	59		
1927	90		
1929	63		
1931	83	1925-31 mean	73.8
1933	38		

Table 2. Pink salmon catches from the Fraser-Puget region, in millions of fish. Figures for 1925-33 are from Table 47 of Rounsefell and Kelez (1938). The 1935-43 catches by Canada are from reports of the British Columbia Commissioner of Fisheries, while those for the United States are from the Pacific Fisherman Statistical Annual, converted at 14 fish per case -- the same factor as used by Rounsefell and Kelez. Figures for 1945-51 are from Annual Reports of the International Pacific Salmon Fisheries Commission.

	USA	Canada	Total		USA	Canada	Total
1925	7.39	1.36	8.75	1939	3.95	1.33	5.28
1927	8.66	1.38	10.04	1941	2.15	1.43	3.58
1929	10.84	1.96	12.80	1943	0.87	0.42	1.29
1931	11.99	0.19	12.18	1945	5.46	1.28	6.74
1933	6.93	1.30	8.23	1947	8.80	3.49	12.29
1935	5.17	1.56	6.73	1949	6.24	3.19	9.43
1937	4.59	1.32	5.91	1951	5.09	2.89	7.97

Table 3. Pink salmon statistics, mostly from Annual Reports of the IPSFC. Colums 2-4: Catches of pinks within the Convention area (Table VIII, 1985 AR). Columns 5-9: Estimates of spawners in Canadian and United States streams within the Convention area (Table XI, 1985; Table XI, 1983; and similar earlier tables). Columns 10-11: Sum of columns 4 and 9, and rate of utilization within the Convention area. Columns 12-15: Estimated spawners in the Fraser River and tributaries; estimated catches of pinks of Fraser origin within and outside of the Convention area; and their total rate of utilization (Tables 8 and 9, 1985). Figures for 1985 and 1987 are from PSCFRP.

	All pink salmon caught or spawning in the Convention area									Fraser pinks				
	Catches			Spawners					Total					
				Fraser										
Year	USA	Canada	Total	Downriver	Upriver	Other Canadian	USA	Total	Total area pinks	Rate of utilization	Spawners	Catch[a]	Total run	Rate of utilization	Year
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1951	5.09	2.89	7.97												1951
1953	4.95	4.14	9.09												1953
1955	4.69	4.13	8.82												1955
1957	2.78	2.63	5.41	1.91	0.33	-	-	2.24+	7.65+	0.71-	2.24	6.15b	8.39b	0.73b	1957
1959	2.43	2.31	4.74	0.97	0.10	-	-	1.07+	5.81+	0.82-	1.07	5.39	6.46	0.83	1959
1961	0.51	0.54	1.05	0.96	0.13	-	-	1.09+	2.14+	0.49-	1.09	0.80	1.89	0.42	1961
1963	4.43	4.17	8.60	1.53	0.42	1.16	3.22	6.33	14.93	0.58	1.95	3.53	5.48	0.64	1963
1965	0.56	0.59	1.15	0.83	0.36	0.16	0.81	2.16	3.31	0.35	1.19	1.13	2.32	0.49	1965
1967	3.83	4.16	7.98	1.14	0.69	0.08	0.73	2.64	10.62	0.75	1.83	11.14	12.97	0.86	1967
1969	0.95	0.86	1.81	1.07	0.46	0.06	0.34	1.93	3.74	0.48	1.53	2.40	3.93	0.61	1969
1971	2.37	2.14	4.51	1.24	0.57	0.11	0.87	2.79	7.30	0.62	1.81	7.95	9.77	0.81	1971
1973	2.22	2.06	4.29	1.22	0.53	0.22	0.60	2.57	6.86	0.63	1.75	5.04	6.79	0.74	1973
1975	1.25	1.26	2.51	0.61	0.76	0.16	0.29	1.82	4.33	0.58	1.37	3.52	4.89	0.72	1975
1977	2.17	2.08	4.24	0.98	1.41	0.04	0.85	3.29	7.52	0.56	2.39	5.85	8.24	0.71	1977
1979	4.05	4.13	8.18	1.96	1.60	0.04	0.78	4.38	12.56	0.65	3.56	10.84	14.40	0.75	1979
1981	3.88	4.19	8.06	2.70	1.79	0.08	0.25	4.82	12.88	0.63	4.49	14.19	18.68	0.76	1981
1983	1.87	1.07	2.94	3.61	1.10	0.03	0.90	5.64	8.58	0.34	4.63	10.72	15.35	0.70	1983
1985	3.86	3.23	7.09	5.97	0.47	-	-	6.44+	13.53+	0.52-	6.46	12.40	18.86	0.66	1985
1987	1.24	0.80	2.04	2.23	1.00	-	-	3.23+	5.27+	0.39-	3.22	3.84	7.06	0.54	1987

[a]Includes Fraser pinks caught both inside and outside of the Convention area.

[b]Figures for 1957 were obtained by estimating the catch in column 13 as bearing the same ratio to the Convention waters catch (column 4) as existed in 1959.

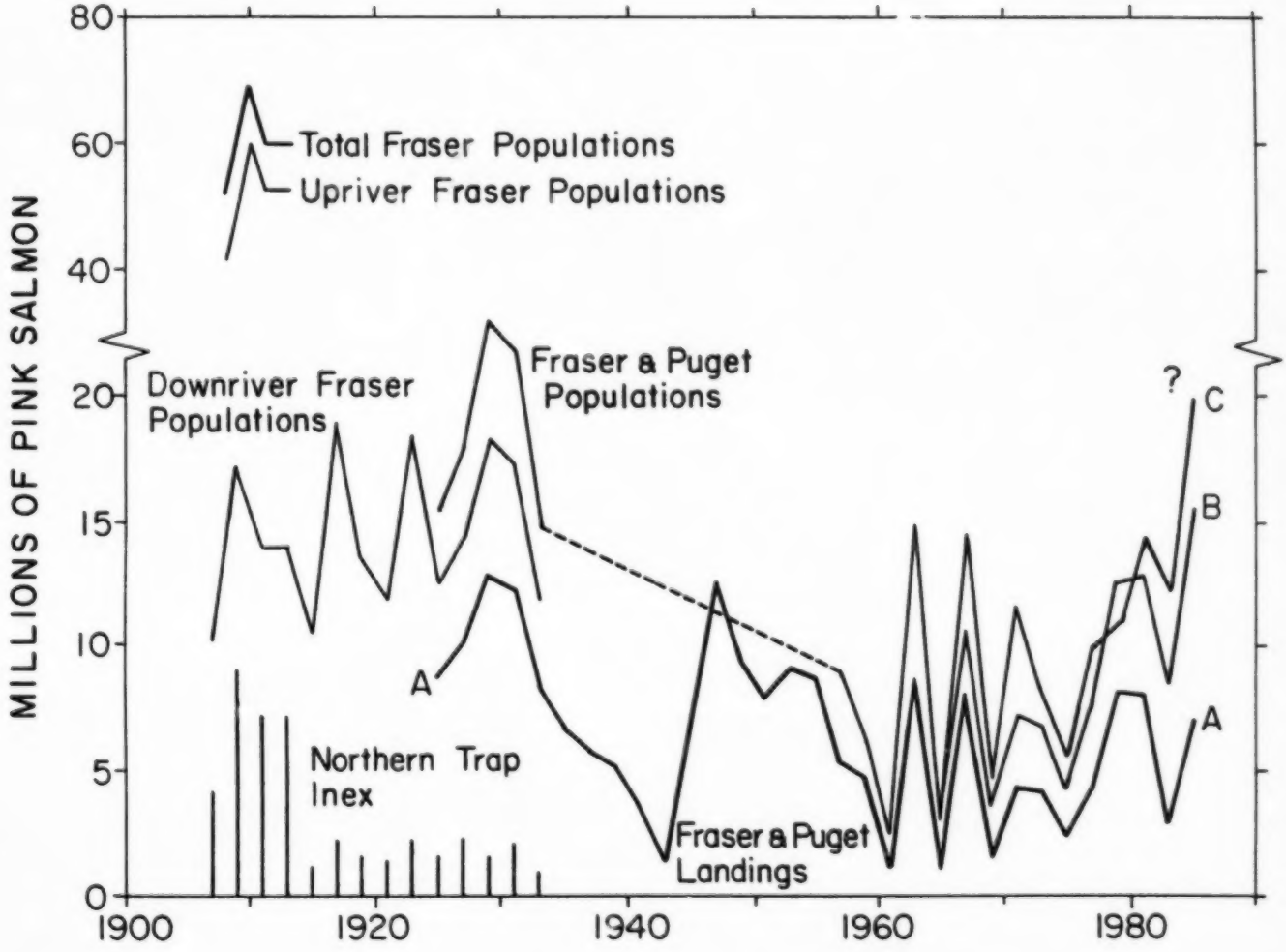
Table 4. Mean weight in kilograms of pink salmon caught in the Fraser-Puget region, caught by different gears. Data from DFO, IPSFC and PSC statistics.

Region:	Juan de Fuca (Area 20)			Fraser (Area 29)	Point Roberts	Southern B.C. (Dist. 1 and 3)
Gear:	Gillnet	Seine	Troll	Gillnet	Seine	All gears
1951	2.74	2.89	2.71	2.85		2.57
1953	2.59	2.69	2.65	2.77		2.53
1955	2.63	2.90	2.79	2.91		2.72
1957	2.41	2.50	2.65	2.57		2.39
1959	2.28	2.38	2.34	2.49	2.40	2.39
1961	2.69	3.09	3.47	3.35	2.99	3.01
1963	2.26	2.30	2.40	2.44	2.34	2.33
1965	2.74	2.87	3.11	2.88	2.82	2.61
1967	2.29	2.41	2.44	2.52	2.45	2.43
1969	2.57	2.63	2.92	2.83	2.73	2.61
1971	2.30	2.27	2.48	2.33	2.35	2.15
1973	2.35	2.44	2.44	2.52	2.45	2.20
1975	2.58	2.72	2.40	2.68	2.74	2.41
1977	2.58	2.63	2.65	2.61	2.67	2.49
1979	2.24	2.19	2.20	2.33	2.29	2.12
1981	2.18	2.23	2.18	2.21	2.19	2.16
1983	-	1.86	-	1.99	2.03	1.81
1985	2.15	2.29	-	2.29	2.22	2.04
1987	2.05	1.98	-	2.16	2.10	2.05

Table 5. Average standard lengths (L) and 60-minute critical swimming speeds at 15 C in lengths per second (L/s) and metres per second (m/s), of pre-spawning Fraser pink salmon in 1983, from downriver sites (Langley and Yale) and from upriver sites (Thompson Canyon, Ashcroft and Seton). From Tables 14 and 15 of Williams et al. (1986).

	Males			Females		
Sites	L(mm)	L/s	m/s	L(mm)	L/s	m/s
Downriver	491	2.34	1.15	465	2.15	1.00
Upriver	487	3.39	1.65	466	2.78	1.30
Difference			0.50			0.30

Fig. 1. Catches and estimates of the total population of pink salmon in the Fraser-Puget region, and Rounsefell and Kelez's index of abundance for the northern traps. Data from Tables 1-3. Line A: Catch from Swiftsure Bank, Strait of Juan de Fuca, Puget Sound, the Fraser River and adjacent Strait of Georgia up to 1955; later it includes the whole Convention area. Line B: Sum of the above catches and the estimated spawning populations, from 1957 onward. Line C: Estimates of the total population, being the sum of Fraser spawners and the estimated catch of Fraser-born pinks from all parts of the coast, increased by twice the estimated number of spawners in Convention streams other than the Fraser (i.e. assuming a 50% rate of utilization for these stocks). See the text regarding the estimates of populations between 1907 and 1933; for this period "Fraser populations" includes a number of small streams north of Deception Pass. Note the change of scale at 40 million fish.


MILLIONS OF PINK SALMON
80
60
40
20
15
10
5
0
1900
1920
1940
1960
1980
Total Fraser Populations
Upriver Fraser Populations
Downriver Fraser Populations
Fraser & Puget Populations
Northern Trap Inex
Fraser & Puget Landings
A
B
C
?
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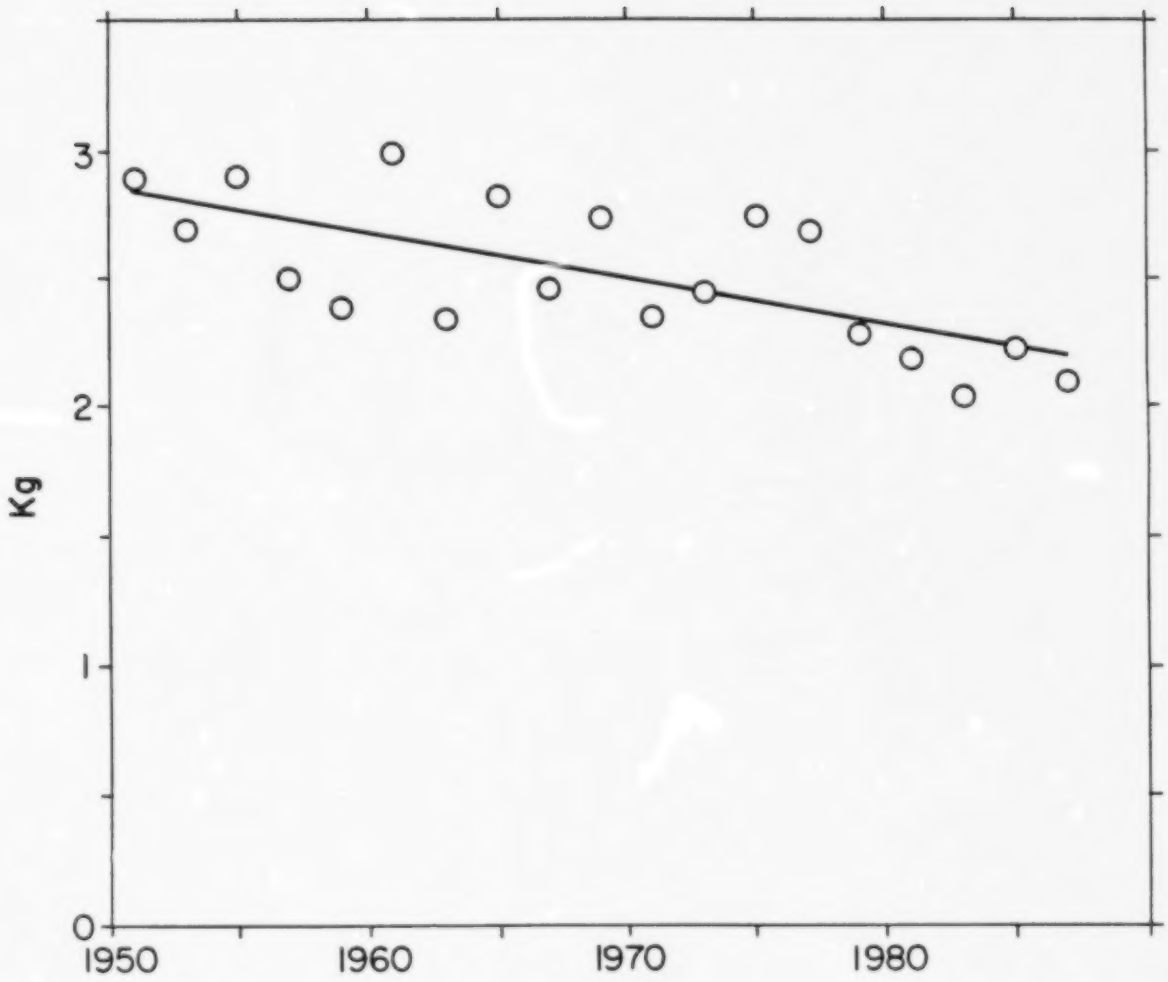

Fig. 2. Mean weight of odd-year pink salmon caught by seine in the Strait of Juan de Fuca (Statistical Area 20) during 1951-57, and near Point Roberts during 1959-87. The linear regression indicates an average decrease of 36 g per generation, 0.64 kg in all. The large fish of 1961 and 1965 occurred in years of very small populations. Data from Table 3.

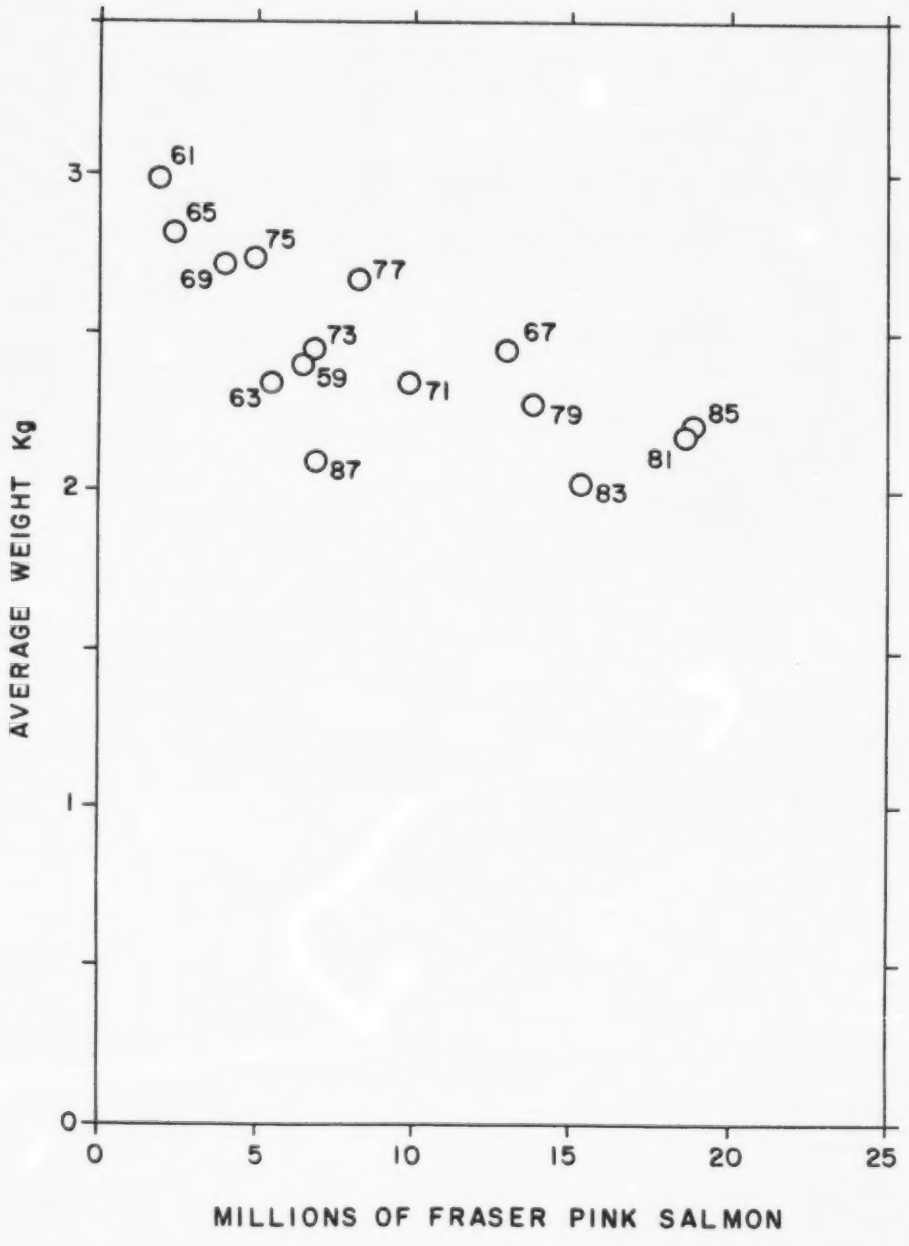

Fig. 3. Average weight of pink salmon in relation to the estimated total abundance of the Fraser-Puget populations. Weight data from Table 4; abundance data from Table 3.

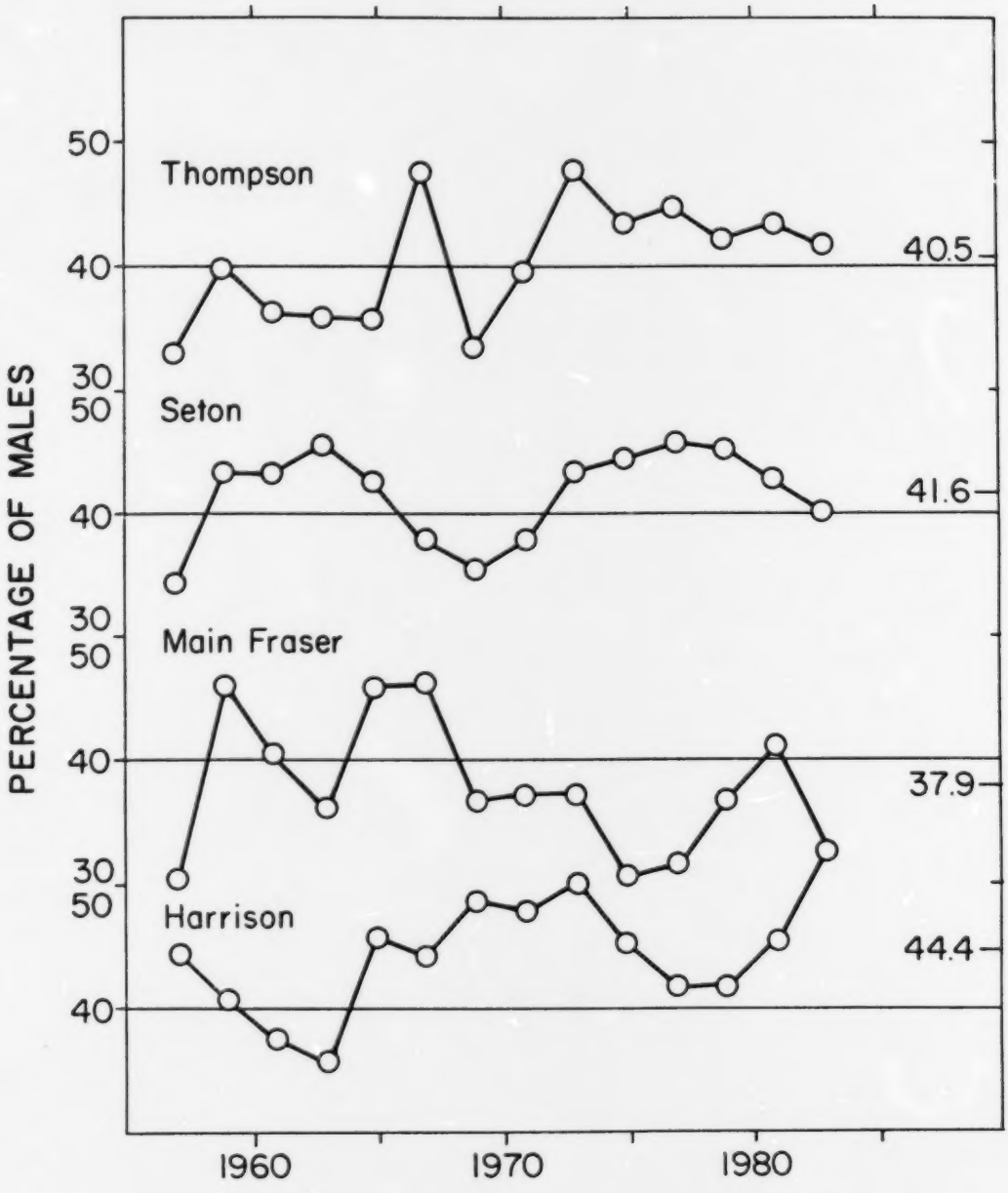

Fig. 4. Percentage of males among the spawners of four pink salmon populations. The Thompson, Seton and Main Fraser populations all belong to the early run, and presumably are subject to fishing of about the same intensity and selectivity. The Harrison is the most numerous of the late-running populations. The 1957-83 average percentages of males are shown at the right. Data from IPSFC, PSCFRP, and CDFO.

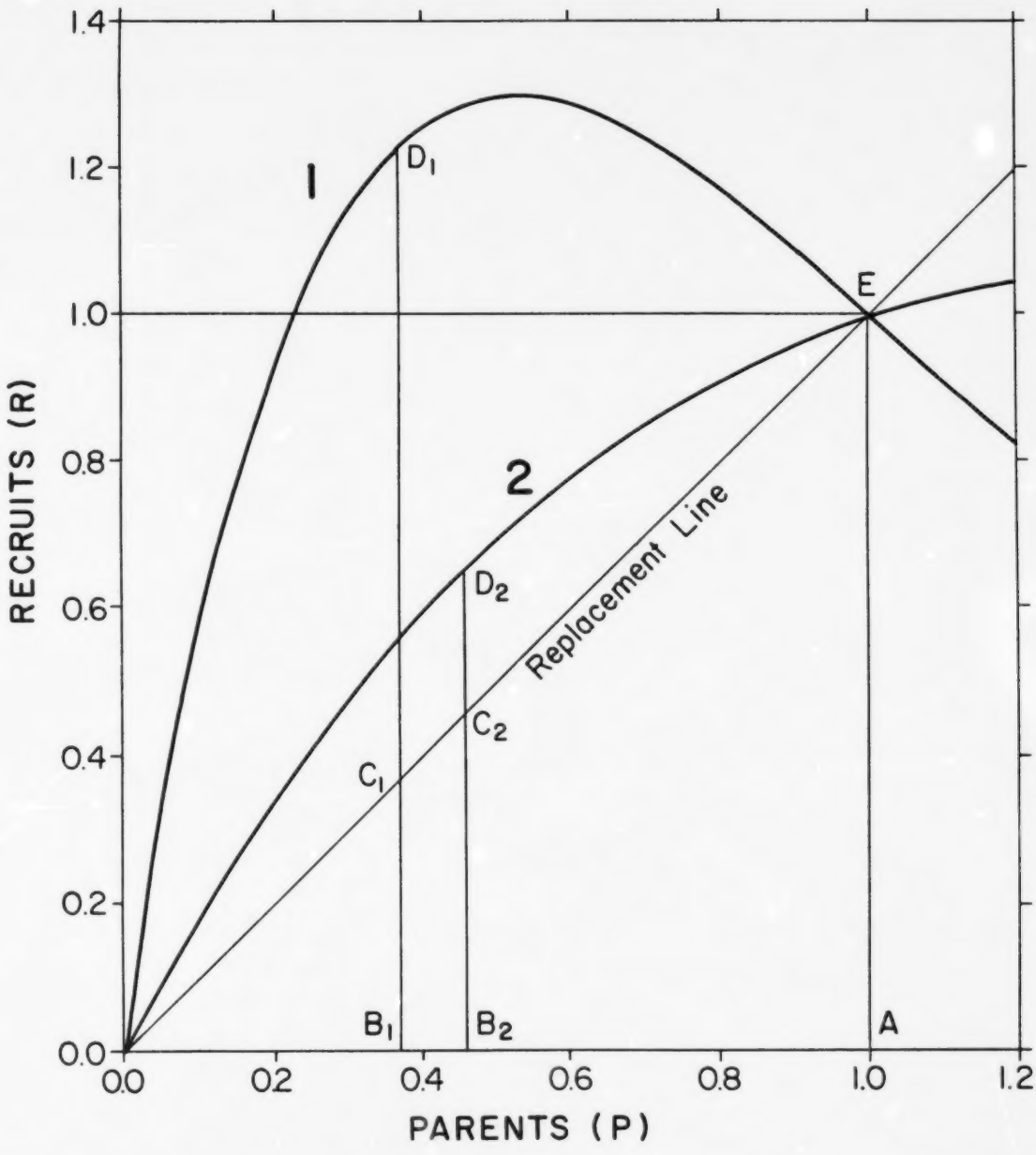

Fig. 5. Two possible recruitment curves for pink salmon (ODE), showing the position of maximum sustainable yield when there is no extraneous variability. For Curve 1 MSY is obtained when the parental stock (OB_1) is 37% as large as its unfished abundance (OA), and the yield (C_1D_1) includes 70% of the total recruits (B_1D_1). For Curve 2 the parental stock at MSY is 46% of OA, and the yield (C_2D_2) can be only 30% of the recruits (B_2D_2). Given that the unfished abundance of parents and recruits (OA) is 1, the equation of Curve 1 is $\ln(R/P) = 1.9040(1 - P)$; for Curve 2 it is $\ln(R/P) = 0.6667(1 - P)$.